

## Influence of eccentric actions on skeletal muscle adaptations to resistance training

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Three different training regimens were performed to study the influence of eccentric muscle actions on skeletal muscle adaptive responses to heavy resistance exercise. Middle-aged males performed the leg press and leg extension exercises two days each week. The resistance was selected to induce failure within six to twelve repetitions of each set. Group CON/ECC ( $n = 8$ ) performed coupled concentric and eccentric actions while group CON ( $n = 8$ ) used concentric actions only. They did four or five sets of each exercise. Group CON/CON ( $n = 10$ ) performed twice as many sets with only concentric actions. Eight subjects did not train and served as controls. Tissue samples were obtained from m. vastus lateralis using the biopsy technique before and after 19 weeks of training, and after four weeks of detraining. Histochemical analyses were performed to assess fibre type composition, fibre area and capillarization. Training increased ( $P < 0.05$ ) Type IIA and decreased ( $P < 0.05$ ) Type IIB fibre percentage. Only group CON/ECC increased Type I area (14%,  $P < 0.05$ ). Type II area increased ( $P < 0.05$ ) 32 and 27%, respectively, in groups CON/ECC and CON/CON, but not in group CON. Mean fibre area increased ( $P < 0.05$ ) 25 and 20% in groups CON/ECC and CON/CON, respectively. Capillaries per fibre increased ( $P < 0.05$ ) equally for Type I and Type II fibres. Capillaries per fibre area for both fibre types, however, increased ( $P < 0.05$ ) only in groups CON and CON/CON. The changes in fibre type composition and capillary frequency were manifest after detraining. At this time only group CON/ECC showed mean fibre hypertrophy, while capillary density was elevated in groups CON/CON and CON. This study suggests that optimal muscle hypertrophy in response to resistance exercise is not attained unless eccentric muscle actions are performed. The data also show that heavy resistance exercise may produce muscle fibre transformation and capillary neoformation.

**Key words:** capillary supply, concentric and eccentric muscle actions, detraining, fibre types and size, hypertrophy, strength training.

Adaptations of the musculoskeletal system to resistive exercise include muscle hypertrophy.

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The increase in muscle cross-sectional area (Narici *et al.* 1989) reflects enlargement of individual cells which is more pronounced in fast-twitch (FT; Type II) than slow-twitch (ST; Type I) fibres (Häkkinen *et al.* 1981, 1985, Komi *et al.* 1982, Houston *et al.* 1983). These adaptive responses appear more prominent when

resistance is provided through gravity-dependent weights, which cause marked variations in muscle shortening or lengthening speed, than when constant speed resistance is applied (Coyle *et al.* 1981, Häkkinen *et al.* 1981, 1985, Komi *et al.* 1982, Côté *et al.* 1988, Pearson & Costill 1988, Colliander & Tesch 1990). Furthermore it has been implicated that the performance of eccentric muscle actions is critical in inducing optimal muscle hypertrophy (Komi & Buskirk 1972). This, however, remains to be proven.

Endurance training may change the myosin molecular structure of muscle. Transformation of Type IIB into IIA fibres, and eventually an increase in the preponderance of Type I fibres at the expense of the fast fibre population may occur (Pette & Vrbová 1985). Cross-sectional studies of heavy resistance trained athletes (Tesch 1987) suggest that the apparent reliance upon Type II fibres during such training does not increase fast fibre composition. Resistance training may, however, increase the relative number of Type IIA fibres on behalf of the Type IIB fibre population (Staron *et al.* 1989, Colliander & Tesch 1990). It is not clear whether the type(s) of muscle action(s) performed has an influence on this response.

Unlike endurance exercise, heavy resistance exercise does not promote an increase in mitochondrial enzyme content (Tesch *et al.* 1987, 1989, Essén-Gustavsson & Tesch 1990). Neither is capillary density enhanced in strength-trained athletes (Schantz 1982, 1983, Tesch *et al.* 1984) nor in response to short-term resistance training (Tesch *et al.* 1983, 1990, Lüthi *et al.* 1986), although some capillary proliferation appears possible in response to resistance training (Schantz 1982, Dudley *et al.* 1986). It is not clear whether the type of muscle action performed in training has an effect on capillary neof ormation or density.

Thus, several questions were addressed in this study. We were interested to study the responses to different heavy resistance training regimens, in an effort to clarify the impact of eccentric muscle actions with respect to possible changes in muscle fibre type composition and size and capillary supply. Because withdrawal of the training stimulus provides an additional opportunity to study the potential mechanisms underlying skeletal muscle adaptations, the individuals participating in this study were reexamined after a short period of detraining.

Greater increases in strength occurred following an exercise regimen comprising coupled concentric and eccentric muscle actions than after training with concentric actions only (Dudley *et al.* 1991a). We hypothesized, therefore, that the former would produce the largest hypertrophic response. It was thought, in contrast, that metabolic-dependent adaptations would occur whether or not eccentric actions were performed because concentric actions mainly account for the increase in energy expenditure during heavy resistance exercise (Dudley *et al.* 1991b).

## MATERIALS AND METHODS

**Subjects.** Thirty-four healthy males, having no formal experience with heavy resistance or endurance training, participated. Their age, height, weight, and treadmill  $\dot{V}O_{2\max}$  averaged ( $\pm$  SE)  $33 \pm 1$  yr,  $177 \pm 1$  cm,  $84 \pm 2$  kg, and  $43 \pm 1$  ml kg<sup>-1</sup> min<sup>-1</sup>. All were screened for health problems that might preclude them from participating in the study. After the procedures, purpose, and risks associated with the study were explained, they provided written consent. The study was approved by the Human Research Review Board at the Kennedy Space Center, FL.

**Training protocol.** Subjects were instructed to maintain their normal activity levels outside of the study. Details of the training program and performance tests have been provided elsewhere (Dudley *et al.* 1991a). Briefly, subjects were accustomed to weight training using bilateral supine leg press and unilateral leg extension by attending three sessions a week on alternate days for 1 month. Subjects were then assigned to one of four groups. Group CON/ECC ( $n = 8$ ) raised and lowered the load for each repetition (rep), and performed 4–5 sets of each exercise with 6–12 reps per set. A one-way hydraulic device that removed the eccentric load, allowed the CON/CON and CON groups to only raise the load, and thus only perform concentric muscle actions. Group CON/CON ( $n = 10$ ) performed 8–10 sets of 6–12 reps, while group CON ( $n = 8$ ) performed 4–5 sets of 6–12 reps. Subjects rested 3 min between sets. They trained 2 days per week for 19 weeks. The leg press and knee extension three-repetition maximum (3-RM), using CON/ECC or CON muscle actions, were performed to assess strength. A control (CTRL) group ( $n = 8$ ) did not train. Subjects were examined before (PRE) and after (POST) 19 weeks of training, and following four weeks of detraining (DTRN).

**Muscle biopsies.** Biopsies were obtained from m. vastus lateralis PRE, POST and DTRN. On each occasion two samples were taken approximately 16–19 cm above the patella using the percutaneous needle method (Bergström 1962). Sampling depth was

**Table 1.** The pretraining fibre area, number of capillaries surrounding muscle fibres, and the number of capillaries per unit fibre area for all groups. Values are mean  $\pm$  SE.

	CTRL	CON/ECC	CON/CON	CON
fibre area ( $\mu\text{m}^2$ )				
type I	4113 $\pm$ 275	4268 $\pm$ 252	4704 $\pm$ 274	4470 $\pm$ 218
type IIA	5796 $\pm$ 404	5666 $\pm$ 297	5831 $\pm$ 313	5850 $\pm$ 368
type IIB	4183 $\pm$ 418	4085 $\pm$ 237	4539 $\pm$ 342	4237 $\pm$ 342
Number of caps surrounding fibres				
type I	4.2 $\pm$ 0.2	3.6 $\pm$ 0.2	3.6 $\pm$ 0.3	3.8 $\pm$ 0.2
type IIA	4.3 $\pm$ 0.2	3.9 $\pm$ 0.2	3.7 $\pm$ 0.3	3.7 $\pm$ 0.2
type IIB	3.5 $\pm$ 0.3	2.9 $\pm$ 0.1	3.2 $\pm$ 0.3	2.8 $\pm$ 0.2
Number of caps per 1000 $\mu\text{m}^2$ fibre type area				
type I	1.06 $\pm$ 0.08	0.87 $\pm$ 0.05	0.78 $\pm$ 0.06	0.86 $\pm$ 0.04
type IIA	0.76 $\pm$ 0.06	0.68 $\pm$ 0.03	0.65 $\pm$ 0.05	0.65 $\pm$ 0.02
type IIB	0.87 $\pm$ 0.07	0.71 $\pm$ 0.02	0.72 $\pm$ 0.06	0.69 $\pm$ 0.06

estimated at 5 cm using biopsy cannulas inscribed in 1 cm increments.

**Sample preparation.** Each tissue sample was oriented for transverse sectioning, affixed to wooden splints using a mixture of O.C.T. compound (Tissue-Tek, Miles Inc., Elkhart, IN) and tragacanth gum, frozen in 2-methylbutane pre-cooled with liquid nitrogen ( $-160^\circ\text{C}$ ), and stored at  $-70^\circ\text{C}$  until processed. Serial sections (12  $\mu\text{m}$ ) of the specimen were cut in a cryostat at  $-22^\circ\text{C}$ .

**Histochemistry.** A given section was assayed in serial fashion for myofibrillar ATPase activity and then the Periodic Acid Schiff (PAS) stain to allow fibre type specific (Types I, IIA and IIB) morphometric and capillary analyses (Hather *et al.* 1991). Adjacent sections were assayed for myofibrillar ATPase at pH 9.4 after acid or alkalin preincubations for classification of Type IIC fibres (Brooke & Kaiser 1970) essentially as done previously (Staron *et al.* 1984). Analyses of the 200 or so biopsies obtained in the present study took over one year. Samples from pre, post and detraining for a given subject were in general analysed at the same time and on occasion resectioned and reanalysed to ensure that variations in the assays or tissue storage did not confound the results.

**Morphometry.** Area and capillarity of the different fibre types were assessed using a semi-automated image analysis system (Hather *et al.* 1991) and muscle fibre type specific area, number of capillaries (CAPS) surrounding a fibre and number of CAPS per unit fibre type area subsequently calculated. Fifty fibres of each type within a localized region were used for area and capillary measurements. Regions of a section were excluded if they contained oblique or histologically

abnormal fibres. In the event that less than 45 fibres of a given type could be measured for a given biopsy, the data were combined with the alternate site to obtain 50 fibres and averaged. The type II fibre area was calculated based on the proportion and area of Type IIA and IIB fibres. Likewise, mean fibre area was determined from fibre type proportion and Type I and Type II fibre area data.

**Statistical analyses.** Statistical analyses were performed using the absolute data obtained for each variable. Each group was analysed separately for each variable using a Three-Way (subject  $\times$  fibre type  $\times$  time) Repeated-Measures ANOVA to examine training effects. Following any main treatment effects with the absence of interaction, pairwise comparisons of the treatment levels were made using a Least Significant Difference (LSD) test. In the case of significant interaction, LSD tests were performed for one treatment over each of the levels of the other treatment. Pre-training data for each variable were compared among groups with a two-way independent ANOVA (group  $\times$  fibre type). All tests of significance were made at the  $\alpha = 0.05$  level.

## RESULTS

The data obtained from the two biopsy sites at any given time showed no systematic differences, thus the values were combined to increase precision (Elder *et al.* 1982). The PRE values for fibre type percentage, fibre area and capillary supply indices were similar for the four groups (Tables 1 & 2). Type IIC fibres occurred so

Table 2. Fibre type percentages in CTRL and experimental groups at PRE, POST and DTRN. Values are mean  $\pm$  SE. \*, different from PRE values  $P > 0.05$ .

	I	IIA	IIB
CTRL			
PRE	45 $\pm$ 2	38 $\pm$ 2	17 $\pm$ 1
POST	39 $\pm$ 3	40 $\pm$ 2	21 $\pm$ 3
DTRN	40 $\pm$ 2	44 $\pm$ 2	16 $\pm$ 2
CON/ECC			
PRE	33 $\pm$ 3	44 $\pm$ 3	23 $\pm$ 2
POST	38 $\pm$ 2	62 $\pm$ 2*	0*
DTRN	34 $\pm$ 2	66 $\pm$ 2*	0*
CON/CON			
PRE	40 $\pm$ 3	42 $\pm$ 2	18 $\pm$ 3
POST	42 $\pm$ 3	57 $\pm$ 3*	1 $\pm$ 1*
DTRN	38 $\pm$ 3	59 $\pm$ 3*	3 $\pm$ 1*
CON			
PRE	33 $\pm$ 3	51 $\pm$ 3	16 $\pm$ 3
POST	37 $\pm$ 3	63 $\pm$ 2*	0*
DTRN	39 $\pm$ 2	58 $\pm$ 3*	3 $\pm$ 2*

infrequently they were not included in analyses. The proportion of Type I fibres remained unchanged over time in all groups (Table 2). All training groups, however, showed decreased ( $P < 0.05$ ) Type IIB percentage and a concomitant increase ( $P < 0.05$ ) in % Type IIA at POST and DTRN. The decrease in Type IIB percentage was of such magnitude that sufficient data for this fibre type could not be obtained after training. Because of this, fibre type specific changes over time are reported for Type I and II fibres.

Mean fibre area increased ( $P < 0.05$ ) 25 and

20% POST in groups CON/ECC and CON/CON, respectively. It remained increased (19%,  $P < 0.05$ ) at DTRN only in group CON/ECC (Table 3). Only group CON/ECC showed increased Type I area at POST and DTRN (14 and 15%, respectively,  $P < 0.05$ ). Type II area at POST and DTRN was increased ( $P < 0.05$ ) 32 and 23% in group CON/ECC. The corresponding increases ( $P < 0.05$ ) in group CON/CON were 27 and 13% (Fig. 1). These groups also demonstrated increases ( $P < 0.05$ ) in Type II/I fibre area ratio at POST which remained at DTRN (Table 3). Groups CON and CTRL showed no significant changes ( $P < 0.05$ ) in fibre area indices over time.

CAPS per fibre was similar for Type I and IIA fibres PRE. Both of these fibre types showed greater values than Type IIB fibres at this time (Table 1). CAPS per unit fibre area was greater ( $P < 0.05$ ) for Type I than Type IIA or IIB fibres PRE (Table 1). CAPS per fibre was increased ( $P < 0.05$ ) similarly for Type I and Type II fibres at POST (Fig. 1). Although this change occurred in all experimental groups, the largest increase was shown in group CON/CON. At DTRN all groups showed increased ( $P < 0.05$ ) CAPS per fibre (Fig. 1). CAPS per fibre area for Type I and Type II fibres was increased ( $P < 0.05$ ) POST in groups CON and CON/CON, and in all groups except CON/ECC at DTRN (Fig. 1).

## DISCUSSION

This study was undertaken to obtain information concerning the design of exercise countermeasures to combat muscle wasting that occurs in weightlessness (Dudley *et al.* 1991a).

Table 3. Type II to Type I fibre area ratio and mean fibre area for groups CTRL, CON/ECC, CON/CON and CON, PRE, POST and DTRN. Values are mean  $\pm$  SE. \* different from PRE values  $P < 0.05$ .

	CTRL	CON/ECC	CON/CON	CON
Type II to Type I area ratio				
PRE	1.34 $\pm$ 0.11	1.21 $\pm$ 0.05	1.18 $\pm$ 0.07	1.25 $\pm$ 0.06
POST	1.32 $\pm$ 0.12	1.40 $\pm$ 0.05*	1.37 $\pm$ 0.04*	1.29 $\pm$ 0.04
DTRN	1.28 $\pm$ 0.05	1.30 $\pm$ 0.03*	1.34 $\pm$ 0.06*	1.20 $\pm$ 0.04
Mean fibre area ( $\mu\text{m}^2$ )				
PRE	4779 $\pm$ 271	4812 $\pm$ 247	5077 $\pm$ 255	5237 $\pm$ 287
POST	5088 $\pm$ 288	5990 $\pm$ 372*	6040 $\pm$ 251*	5839 $\pm$ 618
DTRN	4792 $\pm$ 357	5742 $\pm$ 441*	5372 $\pm$ 248	5282 $\pm$ 457

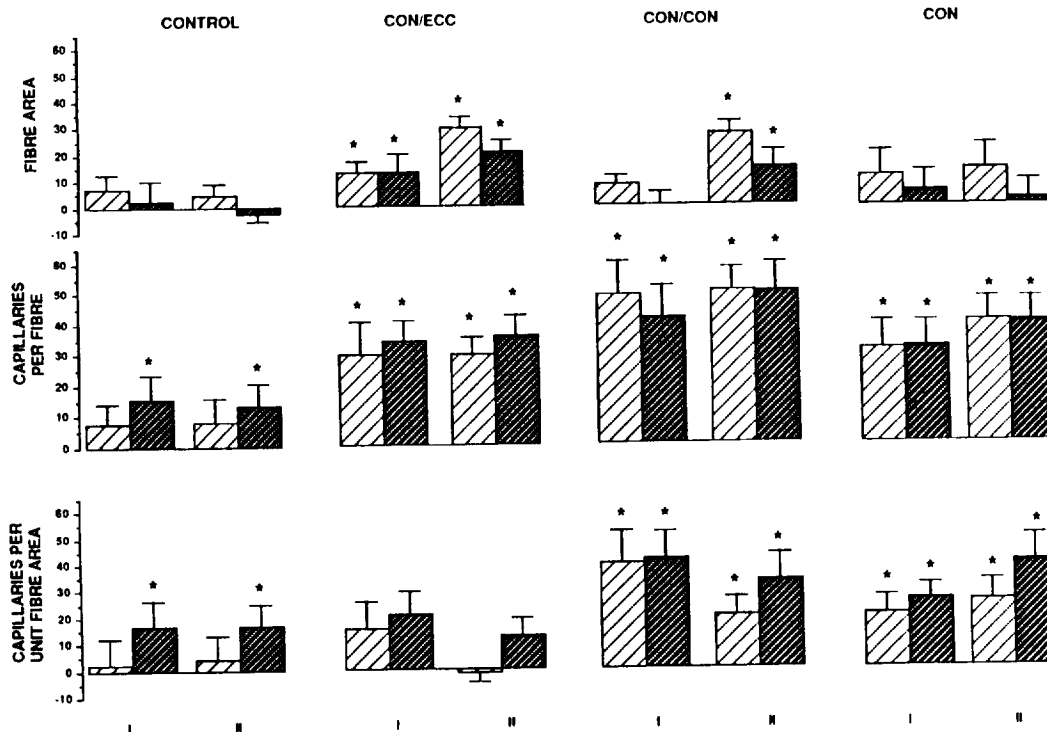


Fig. 1. Effects of nineteen weeks of resistance training with concentric and eccentric (group CON/ECC), concentric and concentric (group CON/CON) or concentric (group CON) actions followed by one month of detraining on Type I or Type II skeletal muscle fibre characteristics. Control group, CTRL. Bars denote relative changes from pre to post-training (▨), and from pre to detraining (■). Values are mean  $\pm$  SE. \*, increase  $P < 0.05$ .

One of the issues was whether performance of eccentric muscle actions is critical in inducing muscle hypertrophy. One subject group, therefore, performed coupled concentric and eccentric muscle actions (CON/ECC), another performed concentric actions only (CON) and a third omitted eccentric actions and performed additional sets (CON/CON) so that the total number of actions became comparable to that of group CON/ECC.

The results suggest that the performance of eccentric actions was critical in optimizing muscle fibre hypertrophy during resistance training, and that the increase in fibre size was better preserved if eccentric actions were used. Only group CON/ECC showed significant increases in mean Type I and Type II fibre area after training. This, in addition was the only group to maintain the hypertrophic response in mean or Type I fibre area after 1 month of detraining.

The mechanisms responsible for these responses are not obvious. Wong & Booth (1990) have recently shown greater enlargement of rat skeletal muscle after a training regimen of artificially induced eccentric, rather than concentric, muscle actions. This was attributed to a more prolonged increase in the rate of protein synthesis with eccentric actions. Whether this was due to the eccentric actions *per se* or because of the greater tension developed during such actions was not determined. It seems likely that eccentric actions optimize the load acted against during training because in the present study group CON/ECC showed a larger increase in the resistance used per set during training than groups CON/CON or CON (Dudley *et al.* 1991a).

Previously it was suggested that to maximize strength increases in response to resistance exercise the performance of eccentric muscle actions is required (Komi & Buskirk 1972,

Colliander & Tesch 1990, Dudley *et al.* 1991a). These studies did not elucidate whether or not the greater increase in strength was due mainly to neural or hypertrophic mechanisms. The results of this study favour the latter explanation. The overall increase ( $P < 0.05$ ) in 3-RM strength, which averaged 28, 22 and 15%, respectively, for groups CON/ECC, CON/CON and CON (Dudley *et al.* 1991a), was comparable to the relative increase in mean fibre area. The 11–25% increases in mean fibre area are within the range of hypertrophy of the quadriceps reported previously (Häkkinen *et al.* 1981, 1985, Komi *et al.* 1982, Houston *et al.* 1983). The finding that the increase in fibre size was comparable to the increase in overall strength has not been reported for previous resistance training studies, but this may have been masked by an inadequate familiarization period.

The finding here of a more pronounced hypertrophy of Type II than Type I fibres in groups CON/ECC and CON/CON is in accord with the vast majority of previous reports where free weights, which require marked accelerative and decelerative force development, have been used (Häkkinen *et al.* 1981, 1985, Komi *et al.* 1982, Houston *et al.* 1983). Training with accommodated resistance and either concentric (Costill *et al.* 1979, Coyle *et al.* 1981, Côté *et al.* 1988, Pearson & Costill 1988, Colliander & Tesch 1990) or coupled concentric and eccentric (Colliander & Tesch 1990) muscle actions, in contrast, has produced no or minute increases in muscle fibre size. Taken together, these results suggest that the type and nature of the muscle action performed influence the hypertrophic response to resistance training.

It is generally accepted that performance of eccentric, but not concentric muscle actions produces delayed onset muscle damage and soreness (Newham *et al.* 1983). The results of this and other studies (Komi & Buskirk 1972, Wong & Booth 1990) may appear controversial, therefore, because they strongly suggest eccentric actions are critical for inducing the hypertrophic response to resistance training. It is uncertain whether delayed onset muscle damage and soreness and the increased breakdown of contractile tissue that occurs after an acute bout of resistance exercise (Dohm *et al.* 1982, Pivarnik *et al.* 1989) are related. Subjects that have been conditioned to perform eccentric exercise do not show appreciable delayed onset muscle damage

and soreness (Fridén *et al.* 1983), yet increased 3-methylhistidine excretion has been reported throughout the course of heavy resistance training (Pivarnik *et al.* 1989). Interestingly, subjects in groups CON/CON and CON, which performed only concentric actions during training in the present study, complained of severe muscle soreness after the post training strength tests with concentric and eccentric actions (unpublished observations). Group CON/ECC did not. This occurred in spite of the facts that groups CON/CON and CON showed positive adaptations to training and the eccentric load during the tests was not maximal, but limited by the preceding concentric action. Thus, eccentric actions appear crucial in optimizing the adaptive response to resistance exercise while minimizing the occurrence of delayed onset muscle damage and soreness. It is not known whether these processes are casually related.

The percentage of Type I fibres did not change as a result of training in the present study, yet all experimental groups demonstrated a marked and uniform increase in the percentage of Type IIA fibres which was paralleled by a decrease in Type IIB percentage. No alterations in fibre type composition were observed in the controls. Thus, training must have induced a transformation in the Type II subtypes. Similar changes, although of smaller magnitude, have been reported following resistance training (Staron *et al.* 1989, Colliander & Tesch 1990). These findings may explain the recent reports of relatively few Type IIB but frequent Type IIA fibres (Staron *et al.* 1984, Essén-Gustavsson & Tesch 1990) and altered Type II myosin heavy chain isoforms (Klitgaard *et al.* 1990) in resistance trained athletes. Hence, an increase in physical activity, not necessarily endurance exercise, may induce a transformation of Type IIB into Type IIA fibres (Pette & Vrbová 1985). This appears to depend on the performance of concentric actions because all training groups in the present study showed this response.

Resistance training for 6–12 weeks has not increased capillary frequency (Tesch *et al.* 1983, 1990, Lüthi *et al.* 1986). The results of cross-sectional studies of competitive weight- and power lifters and bodybuilders also suggest no or modest capillary neoformation as an adaptive response to heavy resistance exercise. It appears, however, that resistance training regimens emphasizing the use of high repetition systems may

induce some capillary proliferation (Schantz 1982, 1983, Dudley *et al.* 1986, Essén-Gustavsson & Tesch 1990). The increase in muscle size typically is larger than capillary neoformation, thus, strength trained athletes possess muscles with a reduced or unchanged capillary density (Schantz 1982, 1983, Tesch *et al.* 1984).

The increase in capillarity after resistance training found in the present study was somewhat surprising. The training induced a marked increase in capillary frequency that was similar for Type I and Type II fibres (Fig. 1). Moreover, the increase was essentially maintained after one month of detraining (Fig. 1). The exact influence of detraining, however, must be viewed with some caution due to the small significant increase found in the CTRL group (Fig. 1). The increase in capillarity after training seemed to correlate with the volume of concentric loading and, therefore, the energy cost of exercise. The largest increase occurred in group CON/CON which executed the greatest volume of concentric resistance at the highest total energy cost (Dudley *et al.* 1991a, b). Groups CON and CON/ECC, which were exposed to comparable concentric loading, showed similar capillary proliferation (Fig. 1). This response was matched by muscle fibre hypertrophy for group CON/ECC such that capillary density was not changed. Groups CON/CON and CON, in contrast, showed increased capillary density as capillary neoformation outweighed hypertrophy.

These findings which are in part at odds with previous work cannot readily be explained. Our subject groups possessed lower aerobic power, i.e.  $43 \text{ ml kg}^{-1} \text{ min}^{-1}$ , and work capacity than others which have been examined prior to training or served as a reference against athletes (Schantz 1982, 1983, Tesch *et al.* 1983, 1984). The potential to increase capillarity, therefore, was probably quite large whatever the exercise stimulus. An adaptation similar to that shown in a sedentary elderly population after moderately intense weight training (Frontera *et al.* 1990) could have occurred. We would, in contrast, rather attribute our findings to the fact that resistance training, i.e. the leg press, was performed in a supine position. This would cause a markedly decreased perfusion pressure in the lower limb during rhythmic heavy exercise in the supine position compared with exercise performed in the erect position (Folkow *et al.*

1971, Eiken & Bjurstedt 1987), and exaggerate muscle ischaemia and hence provide a greater stimulus for capillary proliferation. This suggestion has support in that supine endurance training with substantially reduced limb blood flow induced greater capillary neoformation than training with non-restricted blood flow (Kajiser, L., personal communication).

In summary, the results of this study strongly suggest that maximum rates of muscle protein synthesis in response to heavy resistance exercise, reflected by increased fibre size, are only attained if eccentric muscle actions are used. Alterations in the contractile characteristics and metabolic profile of skeletal muscle, reflected by fibre type composition and capillary supply, in contrast, depend on the extent of concentric loading and thus metabolic stress. It appears that heavy resistance training can induce complete Type II fibre subtype transformation and marked capillary proliferation. It is suggested that these responses may in time attenuate the metabolic stress of the exercise and thereby their prevalence because skeletal muscle of resistance trained individuals does not possess such characteristics.

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